

MODIFICATION OF TRAITS IN MOSAICS FROM BINUCLEATE EGGS OF HABROBRACON ¹

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Egg binuclearity has been suggested to account for the origin of a few rare mosaics in *Drosophila* and of hereditary mosaicism in *Lymantria*. Most of the mosaics which have been found in the parasitic wasp, *Habrobracon juglandis* (Ashmead), are likewise best explained by this hypothesis. The theory advanced by the writer (Whiting, P. W., 1922) is that after extrusion of the first polar body, the second oöcyte nucleus gives rise to two (reduced) nuclei which either take part in parthenogenetic cleavage (male mosaics) or segment after one has been fertilized (gynandromorphs). Post-reduction of binucleate eggs from heterozygous females would then result in mosaic males or, in case of fertilization of one nucleus, in gynandromorphs in which maternal contribution to male and female parts was different.

Mosaics in *Habrobracon* are very infrequent. The present paper is based on 132 mosaic males and 92 gynandromorphs which have occurred scattered through the cultures of various investigators. Whenever a mosaic has been reported it has been given a serial number in the "freak book" with a statement of its origin, a description, and any other pertinent data. The specimen, placed in a gelatine capsule, is then preserved in alcohol for future reference.

MOSAIC MALES FROM HETEROZYGOUS MOTHERS

Virgin females heterozygous for various genes have been bred in tests for linkage. Most of the mosaic males have been found in connection with these studies. They therefore arise from unfertilized eggs and are mosaic for one or more of those traits for which their mothers were heterozygous. It will be convenient first to give a record of these male mosaics as regards the various genes involved.

Females heterozygous for orange, *o* (eyes) (Chromosome I), have produced thirteen sons mosaic for this trait. When tested by mating

¹ The investigations here reported have been aided in part by grants from the Committee on Effects of Radiation on Living Organisms (National Research Council). The drawings for Plate I have been made by Kathryn A. Gilmore.

with orange females two of these mosaics had type (black) daughters, one had orange daughters, and one had both black and orange daughters. The line of division between black and orange ommatidia is difficult to determine, showing more or less gradation. In general the orange regions of eyes of mosaics appear darker than in normal orange and ocelli contain more or less brown pigment so that it is sometimes difficult to classify them as different from "wild type." Ocelli of normal "orange" contain more or less red pigment but not brown, while those of wild type contain much dark brown pigment.

Females heterozygous for ivory, o^i , have produced sons with mosaic eyes which may be classified as follows: nineteen had compound eyes described as mosaic for orange and black; nine for pale orange and black; five had one eye ivory, the other ivory grading through orange to black (Fig. 1); one had one eye black, the other ivory grading through orange to black. Observations were made on ocelli of thirty of these. They were classified as wild type, five; more or less brown pigment, three; very little brown pigment grading to colorless, five; wild type grading to much red pigment, three; more or less red pigment, ten; completely devoid of pigment, four. Breeding tests made of ten of these showed five breeding as black, three as ivory, and two as black and ivory. Twenty showed mosaicism for other traits for which the mothers were also heterozygous.

Females heterozygous for ivory have produced sons showing no very obvious mosaicism in eye color but which were mosaic in other traits of maternal origin affecting wings, legs, or body color. One with eyes and ocelli black bred as ivory; one with ivory eyes and ocelli bred as black and ivory. One with orange eyes and a trace of brown pigment in ocelli bred as ivory. One with orange eyes and ocelli bred as black. Six had pale orange eyes among which one had a trace of brown pigment in ocelli and bred as black; one had much red and brown pigment in ocelli; one had much red pigment in ocelli; while of the other three with colorless ocelli, one bred as black and one as ivory.

Females heterozygous for ivory produced aberrant sons showing no obvious mosaicism in any trait. Eleven of these had eyes classified as orange among which two had colorless ocelli while nine had much red pigment in ocelli. One of the former and six of the latter showed by breeding test that they were actually mutants to orange and one of the latter bred as black and was therefore a mosaic. Seven had eyes classified as pale orange among which one had no pigment in ocelli, two had much red pigment, while four had a small amount of red pigment. One of the last bred as black and was therefore mosaic and one bred as black stumpy and as ivory non-stumpy and therefore had mosaic gonads.

The sixty-two exceptional males produced by females heterozygous for ivory all showed orange modification of eye color to greater or less extent except that one which bred as ivory had black eyes, and one which bred as black and ivory had ivory eyes. The entire group includes forty-four from untreated stock and eighteen from mothers X-rayed as larvæ in twelve cases and as adults in six cases. Among the seven proved by breeding test to be mutants to orange only one was produced by an X-rayed (larva) mother. The seven mutants appeared entirely normal, showing mosaicism in no respect, not even as regards body pigmentation. There is no evidence that X-radiation has caused either modification or mutation to orange.

An orange-ivory compound virgin female, oo^i , produced a male (Fig. 2) with left eye orange, right orange dorsally, ivory ventrally with well-marked line of division between the two regions. Ocelli had red pigment granules characteristic of orange. The specimen bred as ivory.

Females heterozygous for miniature, m (body, antennæ, wings, legs) (Chromosome I), have produced two mosaic males showing clear-cut difference in antennæ, wings, legs, and general body size.

Females heterozygous for cantaloup, c (eye color) (Chromosome II), have produced fourteen mosaic males. Black and cantaloup regions are distinctly marked off in these mosaics in compound eyes and frequently even in ocelli in contrast to gradation observed between black and orange or black and ivory (Figs. 3-9).

Females heterozygous for long, l (antennæ, wings, legs) (Chromosome II), have produced eight mosaic males, one breeding as long. Difference was clear-cut, being evident in antennæ and wings, and could even be noted in legs.

Females heterozygous for narrow, n (wings) (Chromosome II) have produced three mosaic sons with clear-cut difference showing in wings.

Females heterozygous for Minnesota yellow, My (antennal segments) (Chromosome II), have produced five mosaic sons. The character is variable, modified by temperature, but the contrast is striking in antennæ of these mosaics.

Females heterozygous for reduced, r (wings) (Chromosome IV), have produced twelve mosaic sons. Difference is clear-cut and any one wing is either type or reduced. Tests showed four breeding as type and one as reduced. There were likewise produced from heterozygous mothers a reduced breeding as type and a type breeding as reduced, which were therefore also mosaic.

Females heterozygous for fused, f (tarsi, antennæ, wings) (Chromo-

some IV), have produced two mosaic sons. Another male mosaic for fused, found in an inbred culture (No. 3), was in every other respect similar to Stock 3, but proved sterile in observed matings with three females. The method of origin is uncertain, no other fused were found in the culture and it is therefore possible that this may have been a somatic mutant. The combination of traits is unmistakable and this specimen showed typical fused in tarsi, antennæ and wings. Besides this case the locus has been known to mutate four times. Modification of fused in mosaics will be discussed below.

A male mosaic for glass, *g* (eyes and antennæ) (Chromosome IV), occurred in a mixed culture so that parentage is uncertain. The left antenna was very thin as in typical glass, the right type. The eyes were each mosaic with clear-cut regional distinction between glass and type (Figs. 20, 21), but the outline of ommatidia near the margin departs from the normal hexagonal form probably due to absence of pressure from other ommatidia in development. The glass regions are genetically orange, the non-glass black. There is gradation of dark pigment into the orange regions as expected and outlines of bases of abortive ommatidia are rendered visible by the presence of this pigment.

A male mosaic for wavy, *wv* (wings), and a male mosaic for broad, *br* (thorax) (Fig. 16), have each been produced from a heterozygous mother (Chromosome V).

Two males mosaic for white, *wh* (eyes) and one for attenuated, *at* (antennæ) (Chromosome VI), have been produced by heterozygous females. White regions of compound eyes and of ocelli are, as in the case of cantaloup, sharply distinct from black, thus differing from genes in the orange series. (Figs. 10, 11, 12.)

Two mosaics, each with left eye strikingly banded, were produced by mothers heterozygous for ivory and for cantaloup. The normal brothers had eyes of the three expected colors,—black (*OC*), cantaloup (*Oc*), and white (ivory, *oⁱC*, or ivory cantaloup, *oⁱc*). Each mosaic had right eye orange or cantaloup in color which might be genetically cantaloup, *Oc*; ivory, *oⁱC*, modified by the presence of *O* in the mosaic; or ivory cantaloup, *oⁱc*. The last possibility is very unlikely since orange cantaloup, *oc*, is almost white and cantaloup with modified ivory, *oⁱc*, should be no darker. The banded left eyes are shown in Figs. 13 (mosaic No. 550) and 14 (mosaic No. 540). Number 550 shows white dorsally bounded by a sharply marked-off narrow horizontal black band which is split anteriorly by an orange region into which it grades imperceptibly. A broad horizontal white band then follows, sharply marked off from the black lying dorsally, and likewise from a narrow horizontal black line below, which grades ventrally through orange to

ivory. Number 540 shows a somewhat similar pattern (Fig. 14), but the median light band is distinctly pink, "cantaloup." It seems most reasonable to suppose that the sharply marked-off light regions of these eyes are genetically cantaloup, *Oc*, whether they appear white or pink, since eyes of cantaloup stock vary from white to red, becoming progressively darker with age. The grading ivory or orange together with the black bounding bands are then ivory, *o'C*, modified by the dominant allelomorph, *O*, in the cantaloup, *Oc*, regions. It is interesting to note that black color develops despite the absence of wild type, *OC*, tissue. Ocelli of No. 550 were colorless, which may have been either cantaloup or ivory, probably the former. In the case of No. 540, ocelli (Fig. 15) are mixed, the right ocellus as well as the right halves of the median and the left being colorless, "cantaloup." Brown pigment in the left halves of the median and left ocelli indicates modified ivory as in the left compound eye. Asymmetry in ocellar size and in pigmentation of ocellar region is to be ascribed to genetic difference in the tissues involved (Whiting, P. W., 1932).

Females heterozygous for stumpy, *st* (legs) (Chromosome VI), produced fourteen males mosaic for stumpy and three that were modified stumpy and thus suspected of being mosaics. Modifications of stumpy will be discussed below.

Males mosaic for various other traits the genes for which have not yet been shown to be linked have been produced by heterozygous mothers. These include two for semilong, *sl*, showing in antennæ, wings, legs; three for tapering, *ta*, showing in antennæ; one for yellow, *Y* (antennæ); twenty-one for shot vein, *sv* (wing veins); three for club, *cl* (tarsi); three for cut, *ct* (wings); one for indented, *in* (wings); one for attenuated, *at* (antennæ), one for twisted, *tw*, showing in antennæ. Certain males from heterozygous mothers have been suspected of being mosaic for other genes but traits are too fluctuating to assert this with certainty.

ORIGIN OF TRAITS IN GYNANDROMORPHS

Most of the gynandromorphs found in *Habrobracon* are from pure stock or among the progeny of recessive females crossed with dominant males. The reason for this is that they come only from fertilized eggs and that very few offspring are bred from mated heterozygous females or from dominant females by recessive males. By far the greatest number of mated females that have been set are recessive and are used in connection with studies of ratios of biparental males.

Thirty gynandromorphs have been found among progeny of orange-eyed defective, *d* (r_4 wing vein) females crossed with type males. While sex of antennæ can be readily determined, compound eyes vary

considerably in size so that there is no consistent sex difference. Color of eyes is, however, correlated with sex of antennæ. Among the fourteen with both antennæ male, eleven had orange eyes while three had eyes with some mixture of black and orange. Among the fifteen with one antenna male, the other female, eleven had eyes asymmetrical in color with the eye on the female side black, in which case the eye on the male side was orange or mixed; or with the eye on the female side mixed, in which case the eye on the male side was orange. Of the other four cases with asymmetrical antennæ, two had both eyes mixed while two had both eyes black. One wasp with both antennæ female had both eyes black. Male regions of eyes then are orange, matroclinous; female regions show dominant black, patroclinous trait, and are presumably biparental.

Ocelli are larger in male than in female and frequently in gynandromorphs there is asymmetry, the female side showing the smaller ocellus surrounded by integument with characteristically less pigment. Among twenty-seven of these gynandromorphs sixteen had large male ocelli, orange in color, while five had small female ocelli. Six had ocelli asymmetrical in size and color, larger (male) and lighter on one side. In three cases the male ocelli were typically orange while in the other three they had more or less brown pigment. In five cases the female ocelli were described as "black" while in the other one the color was "brown."

Figures 17, 18, and 19 illustrate distribution of pigment in mixed eyes of gynandromorphs from orange females crossed with black-eyed males. Number 373 (Fig. 17) had small (female) black ocelli, and female antennæ. It may be noted that the right eye is black (female) anteriorly. The left eye is orange (male). Number 375 (Fig. 19) is somewhat the reverse with male antennæ, large (male) orange ocelli, while the left eye is orange (male) anteriorly. The right eye is orange (male). Number 397 (Fig. 18) shows a banded condition in the left eye with orange male ocelli, male antennæ, and orange region anteriorly in the right eye. The grading margin may be noted between black and orange in these gynandromorphs in contrast to the clear-cut boundary between black and cantaloup or black and white.

Wings of males are smaller than wings of females. The gene for defective r_4 vein, d , permits fluctuation in the character. Grade 4 denotes the complete absence of the vein from a wing. Heterozygous females frequently show breaks classified as grades 1 or 2. Among the fourteen gynandromorphs with asymmetrical wings, the larger wings (female) had r_4 classified as follows: type 10, d1—3, d2—1, while the smaller wings (male) had r_4 classified: d2—2, d3—5, d4—7. In each

individual the male wing showed the greater defect indicating maternal origin.

We have already seen that mosaic males produced by mothers heterozygous for ivory usually show modification of this ivory color to orange. One gynandromorph (No. 322) from ivory female by black male had female abdomen and male head. Compound eyes were ivory showing no modification although female parts of body presumably were *Oo*^l. Ocelli were male with a trace of brown pigment. Another (No. 481) from a similar cross with head male, thorax and abdomen mixed, likewise had ivory eyes but in this case the ocelli (male) contained red pigment. Another (No. 605) from a female heterozygous for ivory crossed with a black male had male head, female abdomen. Eyes were pale orange, but ocelli (male) were colorless. Another (No. 304) from ivory female by black male had head mixed, abdomen female. Left antenna was female, right male. Eyes were pronounced orange dorsally, black ventrally. Ocelli were male and of light color but showing some brown pigment. Another (No. 296) from a female heterozygous for ivory by an orange male, had one antenna male, the other female. Eyes were ivory, ocelli male and colorless. Other gynandromorphs from crosses of females recessive for various traits by dominant males have shown male structures recessive (matroclinous) in the following cases; two for orange eyes, *o*; three for cantaloup eyes, *c*; three for long antennæ, *l*; one for type recessive to Minnesota yellow antennæ, *My*. Gynandromorphs from similar crosses have shown female structures, ocelli, dominant (patroclinous, presumably biparental), black in five cases of orange and in two cases of cantaloup.

Only four cases have thus far been reported indicating that maternal contribution to male and to female parts is different. These are cases of crosses of heterozygous females by recessive males. One involved reduced, *r* (wings), showing one reduced and one type primary. Three involving orange had black and orange regions in the eyes. Ocelli were orange and female in one (No. 513) so we may suppose the black parts of the eyes were male, the orange female. In the second (No. 602) the larger ocellus (male) was orange, the smaller two (female) were black. In the third (No. 526) the smaller (female) lateral ocellus had no pigment. It was in a darker (male) region. The median and left ocelli contained orange pigment and although large (male) were in a somewhat lighter (female) region.

MODIFICATION BY MOSAICISM OF FUSED AND STUMPY LEGS

The mosaic "mutant" to fused (No. 507) mentioned above had antennæ typical for fused. The left was slightly longer than the right.

Left wings were both type; right were both fused, the primary showing characteristic indentation at tip of radius vein, the secondary shorter than its mate on the left. The three left legs were type; the right showed tarsi with segments typically fused.

The propleuron was darker on the right side which was presumably composed of tissue bearing *f*. Since this specimen came from pure inbred stock it is likely that this pigmental difference is due to the factor *f* itself, in other words *f* is one of a number of genes causing darkening of integumental pigment. This mosaic proved sterile in observed matings with three females.

One of the mosaic males (No. 510) from a female heterozygous for fused had left antenna presumably type, but terminal segments were somewhat fused. Right antenna was fused and rather shorter than the average for this trait (Figs. 22 and 23). Primary wings were type but right secondary was short, probably fused. Left legs were type as was also the third right leg. First and second right legs were fused, the former showing much swelling in femur and tibia as is often the case in fused. Tarsus of this leg had joints completely fused (Fig. 24). Fusion of joints on the second right tarsus was incomplete (Fig. 25) so that it is possible to distinguish the five segments. The mosaic was highly fertile. Tests showed that it bred as wild type.

The other mosaic for fused (No. 490) was produced by a female which was also heterozygous for semilong, *sl* (antennæ, wings, and legs). The wings of this specimen indicate that the two types of tissue present were wild type and semilong fused, for the left wings were both normal while the right showed the combined influence of semilong and fused. Eyes and ocelli were all cantaloup, but this gene does not presumably affect legs or antennæ. Abdomen was normal male but external genitalia were missing (deficiency) except for a small clasper on the right.

Left antenna was type but showing fusion of joints terminally. Right antenna was fused but rather long, perhaps due to the presence of the gene *sl* (Figs. 28 and 29).

The prothoracic right tarsus was type, while all the others were fused but showing more or less segmentation (Figs. 30-34). The metathoracic right was essentially similar to the left. A metathoracic tarsus from stock fused is shown for comparison (Fig. 35).

It is evident that these three mosaics illustrate considerable modification in the fused tarsi. No such difference occurs in fused stock or in semilong fused. Presumably the change in the legs at least is due to mosaicism. Whether the modification of the type (?) antennæ is caused by mosaicism cannot be established from the two specimens.

Deficiency in genitalia of No. 490 may suggest correlated deficiency in antennæ (Whiting, P. W., 1926).

Distribution of type legs as associated with degree of modification of fused may be noted. In No. 507 there is no modification; all the type are on one side, all the fused on the other. In No. 510 all are type on the left. On the right the third leg is type, the middle tarsus much modified fused, while the first is unmodified fused. In No. 490 the five fused tarsi show modification but the middle right which is next to the type first leg is extremely modified in contrast to its mate on the left. The left mate of the type leg shows definite but relatively little modification. These relationships suggest that modification of fused may be greater according to proximity to type on the same side but that there is little if any influence across the median plane. It may be noted that in No. 490 in which there are no type legs on the left, the left antenna is type and the degree of modification is less extreme on this side. Little of significance may be based on these three specimens, but in view of the relationships in modification of stumpy, it is regarded as worth while to call attention to these facts.

In stumpy wasps the tarsal claws are very close to the tibia, the tarsal segments being reduced to minute chitinous vestiges (as in Fig. 39). Examination of over seventy-five specimens showed only six with a small tarsal segment on one or more legs. Legs showing this segment were prothoracic three, mesothoracic ten, and metathoracic one. There is therefore greater tendency for mesothoracic to possess a segment than for the other pairs. Moreover, an individual having a tarsal segment on one leg is likely to have it on others, for four of the six had segments on two legs while two had segments on three legs.

Females heterozygous for stumpy have been bred in X-radiation experiments by Raymond J. Greb. Among the progeny there have been produced fourteen males that were mosaic for stumpy and three which, although not possessing any type legs, showed modification of stumpy and were mosaic for other traits. Modified stumpy legs of mosaics are shown in Figs. 36, 37, and 38.

Of the entire group of seventeen, ten were produced by females X-rayed as adults, while seven were from non-rayed material. The modification of stumpy found in mosaics appears to have no relation to X-radiation of the mother.

Among the fourteen mosaics for stumpy there were thirty-six type legs and forty-eight stumpy. There were only two instances of right and left pairs of type legs but nine of the fourteen mosaics had all type legs on one side, all stumpy on the other. This distribution of type

and stumpy tissue is considered due to the distribution of genetically diverse nuclei in cleavage.

In order to have a quantitative measure of modification of stumpy, the legs of the seventeen mosaics (fourteen mosaic for stumpy) were roughly classified in grades from 0, denoting typical stumpy, to 6 with tarsi considerably over half normal length. The legs of the three mosaics that were not obviously mosaic for stumpy (with no type legs) were grade 0—10, grade 1—3, grade 2—4, grade 4—1.

Stumpy legs that were opposite to type legs were grade 0—23, grade 1—3, grade 2—3, grade 4—3. Stumpy legs that were on the same side as type legs were grade 0—2, grade 2—1, grade 4—7, grade 6—2. It therefore appears that modification of stumpy is due to association with type on the same side and that there is very little if any influence across the median plane.

If the grades of the various stumpy legs are totalled, the twenty prothoracic amount to 19; the twenty-four mesothoracic amount to 45; and the twenty-two metathoracic amount to 12. It therefore appears that mesothoracic are most subject to modification, prothoracic less, and metathoracic least. This order agrees with the six cases found in non-mosaics, but both ratio of legs modified and degree of modification is much higher in mosaics than in non-mosaics.

A HAPLO-DIPLOID MALE MOSAIC

A certain type of male mosaic not previously considered is a logical expectation from the fact that biparental (diploid) males appear in certain crosses and from the theory that a gynandromorph may be produced when one nucleus of a binucleate egg is fertilized.

Shortly after the discovery of the mutation orange, there were found five patroclinous males from orange females crossed with black males, which, although showing no obvious mosaicism, bred as orange and were highly fertile (Whiting, P. W., 1921). The hypothesis was at that time advanced that the "black" parts were haploid and strictly androgenetic. In view of the abundant evidence now accumulated for egg binuclearity and for male diploidism as well as lack of evidence for androgenesis, it seems preferable to regard these patroclinous male mosaics as haplo-diplonts, developing from binucleate eggs in which one nucleus was fertilized and gave rise, not to female parts as in a gynandromorph, but to diploid male parts.

Such a male, actually showing mosaicism, has recently been found and tested by Milton Franklin Stancati. An orange female (Stock 3) was crossed with a black-eyed male. This male was the original mutant

to indented, *in* (wings). In addition to the regular black females—eighteen, and the orange males—nine, there were produced seven black-eyed biparental males, two of which occurred in the same vial (d) with the mosaic (No. 544).

The mosaic was entirely male, with twenty-four segments in each antenna. Eyes were orange, matroclinous, except for black posterior region of the left. Ocelli were symmetrical in size and large (male). There was much brown pigment in left and median. The right had a very small amount of brown pigment (modified orange?). Body pigment was symmetrical.

The mosaic was highly fertile, producing seventy daughters when mated with three females which produced forty-three sons (female ratio 62 per cent). By the two orange mates there were produced fifty-four orange daughters, while by a black-eyed heterozygous sister there were produced ten black and six orange daughters including no indented although three indented males appeared and one non-indented, proving this sister heterozygous as expected. There were also no indented among numerous descendants of the mosaic by the Stock 3 females. The mosaic therefore bred like its maternal stock (No. 3).

Since eight of the twenty-six fertilized eggs developing in the fraternity of No. 544 produced males, a binucleate egg would here have a very good chance of producing a haplo-diploid male mosaic. In view of the fact that eye color alone has generally been used as the criterion of male biparentalism, it is highly probable that haplo-diploid male mosaics have been missed on account of failure of obvious mosaicism, being classified either as normal haplonts or as biparental males. On the theory advanced, their frequency may bear the same relation to gynandromorphs as the frequency of biparental males bears to females, —haplo-diploid male mosaics/gynandromorphs = biparental males/females.

A CASE OF FOUR-STRAND CROSSING-OVER

Mosaic males from binucleate eggs would be expected to possess in their two types of tissue two of the various possible combinations of those genes for which their mothers were heterozygous. Only in those cases, however, in which the two or more pairs of genes affect the same structure can we be sure of what combinations are present. Thus, if eyes are mosaic for type (black) and cantaloup and wings are mosaic for type and long, there is no way of telling which wing is genetically cantaloup or which eye is genetically long. Virgin females heterozygous for long and for reduced have produced mosaic males having wings long on one side, reduced on the other, or having wings wild type on one side,

long reduced on the other. Gynandromorphs have likewise come from reciprocal crosses of orange and cantaloup having eyes type (black) if female, or showing the maternal color if male.

One instance of recombination of genes affecting the wings may be noted as it involves four-strand crossing-over in ovogenesis. In connection with her experiment on the production of impaternate females, Kathryn A. Gilmore bred progeny from a virgin female heterozygous for four factors in Chromosome II, *My/c.l.n*. Minnesota-yellow, *My*, an irregular dominant, affects basal segments of antennæ. It lies well to the left, 20 units \pm , of the factor for cantaloup eyes, *c*. Long, *l*, lying 12 units \pm to the right of cantaloup, shortens wings distally but lengthens antennal segments. Narrow, *n*, about three units to right of long, makes wings narrow. Among the progeny (male) segregating these four factors as expected there occurred a male (No. 552) with Minnesota-yellow long antennæ and cantaloup eyes and ocelli. Left primary wing was narrow (Fig. 26); right, long narrow (Fig. 27) with defective, r_4 , venation. Character of antennæ indicates a crossover somewhere between *My* and *l*. Origin of defective is uncertain and need not concern us. Left primary wing indicates that a crossover occurred between *l* and *n*. The right primary, however, shows a non-crossover combination.

The facts indicate that we are concerned with a two-crossover oöcyte, two strands crossing over between *My* and *c*, the other two between *l* and *n*. There is no evidence for double crossing-over. Crossing-over between two strands in one region does not then prevent crossing-over between the other two in another region. For *My* and *n* we have pre-reduction; for *c* and *l* post-reduction. The two oötid nuclei involved in parthenogenetic cleavage were *My.c.l.n* and *My.C.L.n*, while *my.my.-Cc.Ll.Nn* went out in the first polar body.

SUMMARY

Mosaic males from heterozygous mothers have shown clear-cut mosaicism for the recessive eye colors cantaloup and white. Orange, however, shows intergradation with black of wild type and ivory shows complicated types of modification and intergradation. A similar condition obtains in the case of gynandromorphs. Males have shown clear-cut mosaicism for sixteen other traits. As regards either fused or stumpy legs, however, there is much modification, with evidence that influence is from wild type tissue on the same side of the body, but not on the opposite side. Further evidence is presented indicating that gynandromorphs show maternal traits in male parts of body while female parts are biparental. Maternal contribution to male and female

parts may be different. A male mosaic has been found which is best explained as a haplo-diplont, being in part biparental. A mosaic male from a mother heterozygous for four linked genes indicates such a combination of traits that two crossovers must have taken place in the tetrad, one between two strands, one between the other two, in the egg from which this male developed.

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EXPLANATION OF PLATE I

Figs. 1, 2, 3, 5, 7, 9, 10, 11, 12, 13, 14, 17, 18, 19. $\times 27$. In compound eyes solid black represents black, stippling indicates reddish or orange color, white un-stippled regions are white.

Fig. 16. $\times 17$.

Figs. 4, 6, 8, 15, 20, 21. $\times 64$.

Figs. 22, 23, 24, 25, 28-39. $\times 27$.

Figs. 26, 27. $\times 11$.

Figs. 1-15 show eyes and ocelli of males mosaic for various traits as follows: Fig. 1. Type and ivory (No. 383). Fig. 2. Orange and ivory (No. 341). Figs. 3 and 4. Type and cantaloup (No. 378). Figs. 5 and 6. Type and cantaloup (No. 465). Figs. 7 and 8. Type and cantaloup (No. 351). Fig. 9. Type and cantaloup (No. 593). Figs. 10 and 11. Type and white (No. 601). Fig. 12. Type and white (No. 600). Fig. 13. Ivory and cantaloup (No. 550). Figs. 14 and 15. Ivory and cantaloup (No. 540).

Fig. 16. Mesonotum of male mosaic for broad, *br* (No. 465).

Figs. 17 (No. 373), 18 (No. 397), 19 (No. 375). Heads of gynandromorphs with male regions of eyes orange, female regions black.

Figs. 20, 21. Left and right eyes, respectively, of male mosaic for glass and for orange (No. 549). Stippling indicates brownish pigment. The glass regions are in general orange.

Figs. 22 (left antenna), 23 (right antenna), 24 (right prothoracic leg), 25 (right mesothoracic tarsus) from male mosaic for fused (No. 510).

Figs. 26 (left, narrow) and 27 (right, long narrow) wings of mosaic male (No. 552).

Figs. 28 (left antenna), 29 (right antenna), 30 (left prothoracic tarsus), 31 (right prothoracic tarsus), 32 (left mesothoracic tarsus), 33 (right mesothoracic tarsus), 34 (left metathoracic tarsus) from male mosaic for fused (No. 490).

Fig. 35. Metathoracic tarsus of typical fused male.

Fig. 36. Left mesothoracic tarsus of male mosaic for stumpy (No. 495).

Figs. 37, 38, 39. Two views of left mesothoracic tarsus and one of right metathoracic tarsus of male mosaic for stumpy (No. 497).

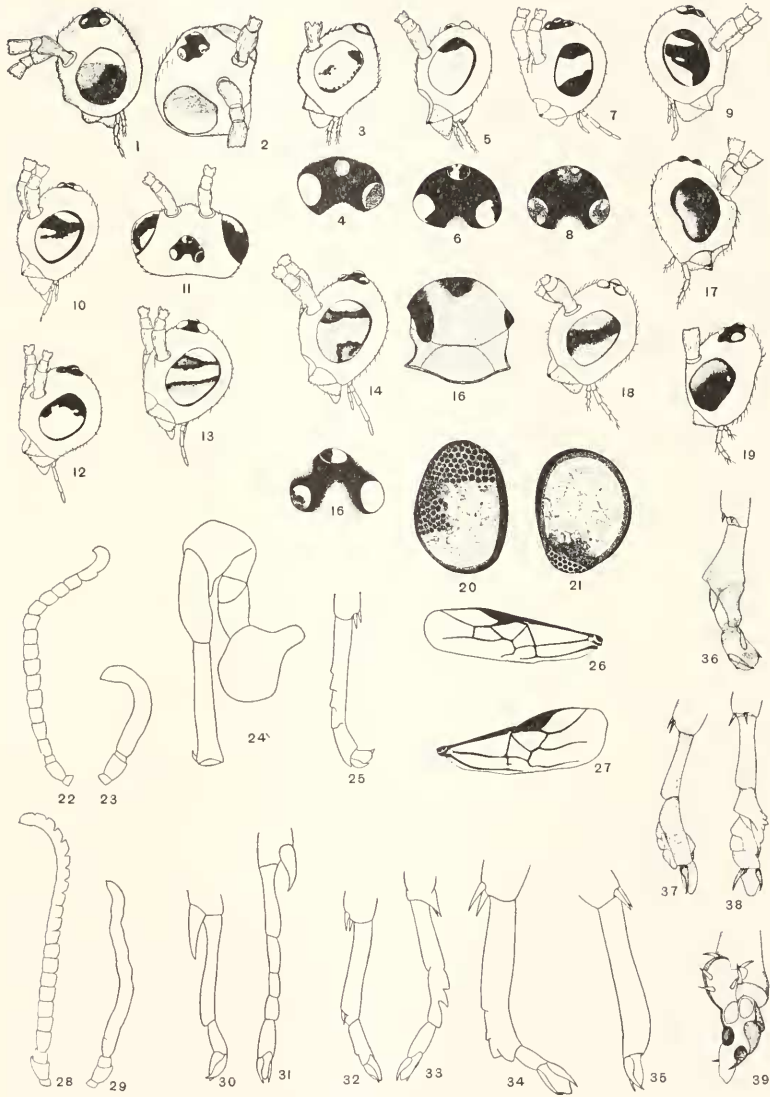


PLATE I